

ESTIMATION OF GENETIC COMPONENTS
OF VARIATION IN SUGAR BEETS
(BETA VULGARIS L.), WITH SPECIAL
EMPHASIS ON EPISTATIC INTERACTIONS.

BY

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Frontispiece : A sugar beet field trial
similar to those that have yielded the
results analysed in this paper.

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1. General introduction.

The ultimate goal of all plant breeding programs is to produce new varieties that are better in one or several characters than the varieties already existing.

Man has since his first days in a civilized community almost totally depended on crop plants to secure his need of food. He thus started selection of types of plants which came up to his desire. Plant breeding started with such simple selections. Later, with the development of scientific genetic crossing programs for selection and variety production, plant breeding was brought up to present level. In hybrid breeding it typically consists of extraction of specific lines from a gene pool, with subsequent selection between lines and combination of the very best few to a hybrid, which is the new variety, as shown in fig. 1 : 1

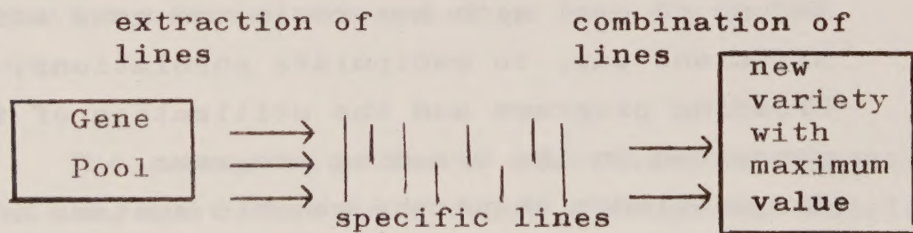


Fig. 1 : After Wenzel (1980) modified

In the case of cross-fertilizing species like the sugar beet most often hybrid varieties are aimed at, according to the above principle. At least if certain prerequisites such as male sterility are at hand.

If this possibility does not exist, other means are used like bulk crossing of selected lines or specific crosses of parental lines.

In all these cases the result of the efforts depends on the exploitation of the heterosis phenomenon.

The knowledge of the existence of heterosis and of its related phenomenon inbreeding depression is very old. But an attempt to scientifically understand the underlying causes was not possible before the development of the science of genetics. The possibility to explain and manipulate heterosis with biometrical and quantitative genetic methods have considerably developed together with the genetic science. But the primary biochemical-physiological underlying causes, in spite of many studies, remain virtually as obscure as they were from the beginning.

The biometrical methods have, however, permitted us to deal with heterosis and gene effects in an efficient way, to manipulate populations, plant breeding programs and the utilization of the lines generated in the breeding programs. Our knowledge about the genetic systems controlling the characters to be selected has thus increased very much due to biometrical investigations.

But quite frequently it is assumed for sake of simplicity that second degree relations such as epistatic interactions are absent,

although knowing that in many cases this assumption is perhaps not entirely true.

In the widely used diallel analysis presented by Hayman (1954 a and 1954 b) the following conditions are presumed :

- 1 Homozygous parents
- 2 Diploid segregation
- 3 No reciprocal difference or maternal effects
- 4 No epistasis
- 5 No multiple alleles
- 6 No linkage and uncorrelated gene distribution
- 7 No genotype-environment interaction.

Most characters of economic interest in the sugar beet are quantitative traits, which are characterized by continuous distribution. This includes both gene effects and effects due to interaction between the genotype and the environment.

The gene action for a quantitative character, like yield, must thus be studied through the metric values and the variation around the mean values. This variation can be partitioned into components attributed to different causes. It is the relative magnitude of these that describes the genetic structure of the population.

On crops in general, and maize in particular, a great number of investigations have been made, but on sugar beets very few.



The present investigation was undertaken primarily, in order to find out if epistatic gene action could be demonstrated to exist in the sugar beet.

Information about eventual presence of epistatic interactions in the sugar beet is of vital importance when making the choice of breeding methods and predicting the outcome of different selection systems.

A second purpose has been to illustrate the importance of the found epistatic effects in composing varieties from selected superior inbred lines. From the works of Bauman (1959), Eberhart and Hallauer (1968) and from Stuber et al (1973) it is suggested that favorable epistatic combinations of genes in inbred lines might contribute to heterosis in crosses in maize (*Zea mays* L.) Genetic recombination in double crosses could result in the disruption of epistatic complexes so that the double crosses did not perform as well as was predicted on the basis of test cross performances.

Both with open-pollinated varieties and varietal hybrids as investigated material, epistatic variability was found to be negligible by several authors, like Compton et al (1965) Eberhart et al (1966), Robinson et al (1958) and Stuber et al (1966).

In contrast, several other authors could find significant epistatic effects in their investigations.

Thus Bauman (1959), Gorsline (1961), Sprague et al (1962) and Sprague and Thomas (1967) in parallel studies found the epistatic effects sought for.

A probable explanation for these indeed contradictory results is that in the first (negative) cases the investigated materials were old, rather unselected, populations, while in the latter (positive) cases, the investigated materials were populations or groups of elite inbred lines, except for the investigation by Sprague and Thomas (1967).

Also in other studies, like the investigations by Cornelius and Taylor (1980) in red clover, in which were used more unselected material, it was found that epistatic interactions were not a major contributor to the heterosis in the red clover single crosses.

Jinks et al (1969) were testing their developed theory of triple test cross with tobacco (*Nicotiana rustica*) and found epistasis at least for some characters.

Stuber and Moll (1971) and Stuber et al (1973) compared the same basic populations in unselected state (UNS) and after three cycles of reciprocal recurrent selection (RRS), they found higher values for epistatic variance for yield components in the selected RRS material than in the unselected UNS material.

This agrees very well with the seemingly conflicting results from the early investigators cited above. Selected material shows a higher proportion of the genetic variance as epistatic variance than do the unselected populations.

The important points to investigate follow from the above : Does epistatic interactions occur in highly selected lines of sugar beets from which we intend to construct new varieties ? Under which conditions can this construction be made ? These questions correspond to the step " combination " in Fig. 1 : 1 above.

Also it was felt important that an investigation was made with more than one method and more than one set of materials. Evidences for presence of epistasis in maize have been sought for a number of times by several authors, with conflicting results.

The present investigation uses two different methods for epistatic interaction detection.

Firstly the Triple Test Cross as described by Kearsy and Jinks (1968) and secondly a Generation Mean Study, also called the Scaling Test. The latter method was described by Hayman (1958 and 1960) and is used as described by Mather and Jinks (1982).

Three sets of materials are used, two with the Triple Test Cross, and one with the Generation Means Analysis.

Also several locations and several years have been used for the field testing in order to gain more generality of the results.

2. DEFINITION OF EPISTATIC INTERACTION AND A BRIEF HISTORICAL NOTE.

Epistasis is a term defined in the classical Mendelian genetics to describe the effects of genes whose effects mask or cover the effects of other genes. In this sense and definition, the term was introduced by Bateson (1909) to describe the effects which caused the observed 9:3:3:1 segregation ratios to appear as 9:3:4 or 12:3:1 in the F_2 following a cross.

This classical definition of epistatic interactions must not be confounded with the much broader and more general definition of epistasis as a term in the quantitative or biometrical genetics. In this context the term describes interactions between genes at different loci, where the effect of one gene changes according to the presence or absence of another gene or genes.

These epistatic interactions comprise several different types of interactions such as complementary, supplementary, duplicative, multiplicative, and possibly other forms of interaction (Singh, 1973)

Also epistatic interaction must be carefully distinguished from dominance, which refers to non-additivity of alleles at the same locus.

There seems to be no really generally accepted term. Several terms meaning the same are in general use.

In the literature we thus find the terms

Epistacy

Epistasis

Epistatic interaction

Non-allelic interaction

Inter-allelic interaction

which are, by different authors, used to describe the same genetic relationship and are thus synonyms.

In the present work I have chosen the term "Epistatic interaction".

The first biometrical treatment of epistatic interactions was given by Fisher (1918), but very little was considered for about thirty years. Wright (1935) made some developments for a special model, but it was not until the 1950's that work really started. Cockerham, Anderson and Kempthorne then developed the theory in the years 1950-1954. Especially the terms additive x additive, additive x dominance and dominance x dominance were first given by Cockerham (1952,1954) and he worked out the case for two alleles per locus with arbitrary gene frequencies.

Epistatic interaction effects in connexion with inbreeding and populations derived from inbred lines were treated and developed by Horner (ref. in Kempthorne 1957) and by Hayman and Mather (1955).

Kempthorne has given a more mathematical treatment in his book *An Introduction to Genetic Statistics*. (1957)

3. Survey of literature

The development of biometrical methods and knowledge of gene action and gene interaction, as seen and handled in the biometrical sense, has greatly increased during the last 20-25 years, that is since about 1960. This is especially true for the type of gene interaction which we call epistasis, or epistatic interaction.

Although the term was coined by Bateson in 1908 in studying qualitative traits, and discussed in a biometrical sense by Fisher already in 1918, its proper analysis and statistical treatment were lacking. Wright (1918) also contributed to the discussion and development of biometrical-statistical methods regarding epistatic interactions.

Indeed, in the beginning the biometrical methods regularly had as one of their mathematical assumptions that epistasis was absent. A good example is the diallel cross, as developed by Hayman (1954). The diallel cross and its analysis to gain information about the functioning of the genetic system has been especially widespread, and has been used in very many different crops.

In all these performed analyses of genetic systems the underlying assumption is the absence of epistasis.

This absence of epistatic interactions, one soon found out, is not always true. In fact quite often the opposite is true.

The arrival of new genetical designs with their proper statistical analysis greatly improved the situation. Notably the so called North Carolina Designs I, II and III as proposed by Comstock and Robinson (1948 and 1952) and the diallel cross first analyzed with statistical technique by Sprague and Tatum (1942).

However, the interest centered at first around the additive component, presumably because it is the most easily handled, in its detection, estimate and use in the breeding work. Most of the genetic models could, in fact, only judge the relative importance of additive and dominance components. This is the case for the above-mentioned works by Comstock and Robinson (1948 and 1952), as is also true for Hayman's (1954) analysis of the diallel cross, and for Jinks (1954) work on *Nicotiana*.

The development of the so called scaling tests, where a number of specific generations are produced by crossing gave possibility for more precise estimation of the relative importances of additive, dominance, additive x additive, additive x dominance and dominance x dominance variance components. The works by Anderson and Kempthorne (1954), Cockerham (1954) Hayman (1958 and 1960) and Jinks and Jones (1958) led to the development of this crossing system and its interpretation as presented by Gamble (1962 a and 1962 b).

The other important development was the extension of the North Carolina Design III method to the so called Triple Test Cross as presented by Kearsy and Jinks (1968). With this test cross, it is possible to eliminate the additive and dominance components of variance, and leave only the epistatic ones. The different types are confounded, however. But on the other hand it is possible to investigate any population, irrespective both of its gene frequencies and its mating system. The tested material can, furthermore, be on any level of inbreeding in contrast to most other designs, which demand homozygous parents.

In Birmingham, a group of people continued to develop the Triple Test Cross in various aspects and tested the variation on *Nicotiana rustica* material at hand in Birmingham. Thus the application to inbred lines was presented by Jinks et al (1969), the application to F_2 and backcross populations by Jinks and Perkins (1970), to normal families and their selfs by Pooni et al (1980).

Induced variation, i.e. variation induced by gamma radiation in an F_2 population from two *Nicotiana rustica* inbred lines, was also tested by the Triple Test Cross. Virk et al, 1981). They could easily detect interesting changes in additive and dominance variation, as a result of the irradiation, whereas the epistatic component remained almost unaffected.

The constitution of the testers is important for the efficiency of the Triple Test Cross test. The favourable alleles can be associated in one of the testers, or they can be dispersed between the two testers :

$$\left. \begin{array}{l} P_1 = AABB \\ P_2 : aabb \end{array} \right\} \text{ (associated)}$$

or the type

$$\left. \begin{array}{l} P_1 = AAbb \\ P_2 = aaBB \end{array} \right\} \text{ (dispersed)}$$

With dispersed testers together with linkage disequilibrium we obtain too low estimates of the dominance component, if we have repulsion linkages between alleles whose dominance deviations have the same sign. The epistatic component is well detected both with associated and dispersed testers, but with higher levels of significance if the testers are associated.

A number of other methods are possible to use when one wants to estimate components of genetic variation. For example S_1 inbreds can be used to estimate additive variation (6_A^2). In case of presence of epistasis we will have the estimate $6_A^2 \times 6_{AA}^2$ as the result. (Pooni et al 1978)

The diallel analysis has been used to estimate gene action in many crops, also sugar beets. Smith et al (1973), Theurer et al (1975)

calculated the additive variance and the non-additive variance from general combining ability and specific combining ability (GCA and SCA) estimates. This can be done from the GCA and SCA variance estimates as outlined by Griffing (1956). They found rather big proportions of non-additive variation, for root weight more than 50 % of the variation was non-additive. In this case additive variation comprises σ_A^2 and σ_{AA}^2 components, and non-additive $\sigma_D^2 + \sigma_{AD}^2 + \sigma_{DD}^2$ variance components.

Less pronounced, but in significant amounts Smith et al (1973) found non-additive effects in 10 other characters in sugar beets.

The studies by Theurer et al (1975) on respiration rate, indicated that this character was conditioned both by additive and non-additive gene action.

All this indicates, but does not prove, that epistasis plays an important role in all characters in the sugar beet.

Similar information is gained from comparisons of predicted and realised performances of double cross hybrids from single crosses. In this case, if gene action was additive ($\sigma_A^2 + \sigma_{AA}^2$) the double cross would be exactly predicted by the single crosses. If its performance deviates from the prediction, it must be due to non-additive effects, which thus incorporate epistatic effects (σ_{AD}^2 and σ_{DD}^2).

Studies by Nielson et al (1969) showed such deviations for root yield. Also in a study by Smith and Hecker (1971) several cases are presented where important deviations exist between predicted and observed double cross performance, especially regarding root yield, but also sugar % and purity % (a function of K^+ , Na^+ and Nitrogen levels in the extracted juice)

Mac Lachlan has, in several studies on populations of monogerm sugar beets with several methods, investigated the genetic parameters. In the first study Mac Lachlan (1972 a) used sib analysis of mother line progenies, and could only gain estimates on the additive component ($V_A + V_{AA}$) without estimate on levels of other parameters.

In a second study Mac Lachlan (1972 b) studied offspring-parent regressions of mother line progenies. In this case an estimate of non-additive ($V_D + V_{AD} + V_{DD}$) was also possible. For root yield he found very large quantities of non-additive variation and only small quantities of additive. The sugar content had about equal amounts of additive and non-additive variation.

In his 3rd study Mac Lachlan (1972 c) used the diallel crossing scheme for the estimation of genetic parameters. He found that only root yield and sugar content had significant levels of non-additive variation. These were, on the other hand, large.

Authors often generalize too much when referring to general combining ability as additive effects and specific combining ability as non-additive genetic effects. The real expectation of the components of variance are, according to Matzinger et al (1959)

$$\sigma_g^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{1}{64}\sigma_{AAA}^2 \dots$$

$$\sigma_s^2 = \frac{1}{4}\sigma_D^2 + \frac{1}{8}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AD}^2 + \frac{1}{16}\sigma_{DD}^2 + \frac{3}{32}\sigma_{AAA}^2 + \dots$$

Only in the total absence of epistatic interaction effects are the statements entirely true, but if epistasis is present, the two combining ability effects have to a certain degree components in common, as can be seen from the formulas.

The need for continued investigations with specially constructed crossing series, like the scaling tests as described by Mather and Jinks (1982), and Gamble (1962) would be most useful. The latter test provides values on the following genetic effects :

additive
dominance
additive x additive
additive x dominance
dominance x dominance

Information about the different trigenic and higher orders of epistatic gene interaction is not given. With a more elaborated crossing scheme it could be obtained, however.

The Triple Test Cross (TTC) on the other hand, can provide estimates on all types of epistatic interactions, also tri-genic and higher orders of epistatic interactions, but can not distinguish between the different types of them. Thus, what we receive from the test is an estimate of the total epistatic gene interaction.

4. VARIANCE COMPONENTS, AND THE DECOMPOSITION OF THE GENETIC VALUE .

Adapted from Bulmer (1980), Cockerham (1980) and Mather and Jinks (1982).

4.1. VARIANCE COMPONENTS

When a metric character is studied, one obtains a series of values from measurements, that can be characterized by a mean value and a measure of the variation around this mean.

This variation around the mean can be measured by the variance = V .

Variance can be due to different causes that can be partitioned and identified in the following way :

V_P = The observed phenotypic variance
 V_G = The genetic variance
 V_E = The environmental variance

which have the following relationship

$$V_P = V_G + V_E \quad (4.1)$$

This permits us to separate out the effects, that are due to the genotype from those, that arise from variations in the environment.

The genetic variance, V_G , can in its turn be further partitioned into its genetic components due to different types of genetic effects :

V_A = Additive variance
 V_D = Dominance variance
 V_I = Interaction variance

with the relation :

$$V_G = V_A + V_D + V_I \quad (4.2)$$

Likewise, the V_I component can in its turn be further partitioned into its components in the following way :

V_{AA} = Additive x Additive variance
 V_{AD} = Additive x Dominance variance
 V_{DD} = Dominance x Dominance variance

which, in analogy to the above, have the following relationship :

$$V_I = V_{AA} + V_{AD} + V_{DD} \quad (4.3)$$

This latter expression describes the interaction between genes at two different loci. To describe the situation if we also have interaction between three loci, we have to add the following terms :

$$+ V_{AAA} + V_{AAD} + \dots + V_{DDD} \quad (4.4)$$

and for a 4-locus interaction

$$+ V_{AAAA} + V_{AAAD} + \dots + V_{DDDD} \quad (4.5)$$

and so on.

However, the crossing series and the testing procedures to estimate these components with a reasonable degree of accuracy will be rather complicated and voluminous . In this study, then, it has been necessary to limit the analysis to a two-locus model.

If we now put all these partitioned terms in the same formula, we obtain :

$$V_G = V_A + V_D + V_{AA} + V_{AD} + V_{DD} \quad (4.6)$$

4.2. DECOMPOSITION OF THE GENOTYPIC VALUE

To explain the meaning of the partition of variances made in section 4.1, consider an illustrative example of a case with two loci. The decomposition is, according to BULMER (1980) :

$$\begin{aligned} G = M + & \left[(X_1 + X_3) + (X_2 + X_4) \right] + \\ & + \left[X_{13} + X_{24} \right] + \\ & + \left[X_{12} + X_{14} + X_{23} + X_{34} \right] \\ & + \left[(X_{123} + X_{134}) + (X_{124} + X_{234}) \right] + \\ & + \left[X_{1234} \right] \end{aligned} \quad (4.7)$$

where

G = the Genotypic value

M = the mean value

$(X_1 + X_3)$ = the main effects of the two genes at the first locus. Their sum is denoted by A_1 and is called the additive component at the first locus.

$(X_2 + X_4)$ = similarly, the additive component at the second locus, and is denoted by A_2 .

X_{13} = the interaction between the main effects at the first locus, and is usually called the dominance deviation at the first locus, denoted by D_1 .

X_{24} = in the same way the dominance deviation at the second locus, denoted by D_2 .

$X_{12} + X_{14} + X_{23} + X_{34}$ = are interactions between the main effects of a gene at the first locus and the main effects of a gene at the second locus. The four terms represent the four relations possible. The sum of these is denoted by AA_{12}

$X_{124} + X_{234}$ represent interactions between the main effects of a gene at the first locus with dominance deviation at the second locus, denoted by AD_{12} .

$X_{123} + X_{134}$ is likewise defined, and denoted by AD_{21}

X_{1234} = the interaction between the dominance deviations at the two loci, and we denote by DD_{12} .

This can be put together to reconstruct the formula (4.7) :

$$G = M + (A_1 + A_2) + (D_1 + D_2) + AA_{12} + (AD_{12} + AD_{21}) + DD_{12} \quad (4.8)$$

and if we group the terms together, it becomes :

$$G = M + A + D + AA + AD + DD \quad (4.9)$$

The variation between the genotypic values as recorded in the trials will then be :

$$V_G = V_A + V_D + V_{AA} + V_{AD} + V_{DD} \quad (4.10)$$

which is identical to what we observed at the partitioning of the variance components. (equation 4.6)

where

- A = the additive genetic value of the genotype
- D = the total dominance deviation
- AA = the additive x additive interaction
- AD = the additive x dominance interaction and
- DD = the dominance x dominance interaction

4.3. EXAMPLES OF DECOMPOSITION OF THE GENETIC VARIANCE INTO COMPONENTS.

For the purpose of illustrating the present investigation by a numerical example, consider the two following populations from Bulmer (1980) :

A single locus with two alleles, B and b, with B completely dominant over b. Allele frequencies : $B = b = 0.5$

Genotype	BB	Bb	bB	bb
Frequency	0.25	0.25	0.25	0.25
Genotypic value	1	1	1	0

The decomposed genetic variance, V_G will be as follows :

$V_A = 0.125$
 $V_D = 0.0625$
and $V_G = 0.1875$

A two locus model with complementary gene action, i.e. showing complementary epistatic effects.

		BB	Bb	bB	bb	G 24
Genotypic values	CC	1	1	1	0	0.75
	Cc	1	1	1	0	0.75
	cC	1	1	1	0	0.75
	cc	0	0	0	0	0.00
	G 13	0.75	0.75	0.75	0.00	

The corresponding decomposition of the genetic variance, V_G :

$V_A = 0.1406$
 $V_D = 0.0703$
 $V_{AA} = 0.0156$
 $V_{AD} = 0.0156$
 $V_{DD} = 0.0039$

which makes the total = $V_G = 0.2461$

In this context it has to be noted that each locus is showing complete dominance :

We have $BB = Bb = bB = 0.75$ and $bb = 0.00$

For locus C we have an identical relationship.

The epistatic effects that are estimated in the following Experiment I, are the sum of the genetic effects : AA, AD and DD, whereas the main effects and the dominance deviations, i.e. the A and the D components, are cancelled out.

Estimated in Experiment I is thus :

$$I = AA + AD + DD$$

supposing a two-locus system.

In Experiment II all five components are estimated,
i.e.

$$A + D + AA + AD + DD$$

5. EXPERIMENT I.

5. THE TRIPLE TEST CROSS TEST

a) Introduction

Function of the tester sets.

The Triple Test Cross is an efficient method to analyse and study the genetic structure of a genotype with the regard to presence or not of epistatic interaction between the genes.

The tester sets consists of two inbreed lines, which form the testers L_1 and L_2 , and the F_1 hybrid between them, which forms the L_3 tester.

This experimental method overcomes the difficulties encountered in many methods for estimating genetic effects, namely to offer an unbiased estimate of the epistatic interaction. These difficulties include calculation of second degree statistics and the large standard errors that are associated with statistics. Further, the methods are often sensitive to linkages and correlated gene distribution in the parents.

Kearsey and Jinks (1968) presented the Triple Test Cross method, which is a method with general validity for investigating any population, in that it is insensitive to both gene frequencies, mating system or level of heterozygosity.

Still following Kearsey and Jinks, let us assume K loci where we have genetic variation within the population of lines to be tested, and of these, K' (where $K' \leq K$) differ between L_1 and L_2 .

If now $K' < K$, that is the testers are not as widely chosen as theoretically possible, the test for epistasis will not be invalidated, but will instead detect epistatic interactions between these K' loci, and the same would be true for a dominance effects estimation.

If one assumes that these K' loci are a random sample of the loci segregating in the population, then this analysis will indicate whether or not epistatic interactions and dominance are components of the genetic architecture, but will not indicate their absolute contribution. Epistatic interaction could exist between loci for which the testers are homozygous, but this will then not be detected. Significant values for epistatic interactions would thus be a proof of their existence, but the reverse is not true : No detected epistatic interactions is no proof that they do not exist.

Test for epistatic interactions.

To illustrate the test, let us consider the situation when $K' = 2$. The Table 5:1 shows the expected mean values of the tester sets, derived by crossing each of the 9 possible genotypes, in the case of 2 loci with three testers.

TABLE 5:1

The contribution of main effects and digenic interaction parameters to the means of L_{1i} , L_{2i} , L_{3i} and $L_{1i}+L_{2i}-2L_{3i}$ for each of the 9 possible genotypes in respect of genes A-a and B-b. Adapted from Kearsey and Jinks (1968).

(a)	L_1 (AABB)							L_2 (aabb)							L_3 (AaBb)						
	a_A	a_B	d_A	d_B	aa	ad	dd	a_A	a_B	d_A	d_B	aa	ad	dd	a_A	a_B	d_A	d_B	aa	ad	dd
AABB	1	1	-	-	1	-	-	-	-	1	1	-	-	1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$
AABb	1	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	-	$-\frac{1}{2}$	1	$\frac{1}{2}$	-	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{4}$	$\frac{1}{2}$
AAbb	1	-	-	1	-	1	-	-	-1	1	-	-	-1	-	$-\frac{1}{2}$	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$-\frac{1}{4}$	-	$-\frac{1}{4}$
AaBB	$\frac{1}{2}$	1	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-	$-\frac{1}{2}$	-	$\frac{1}{2}$	1	-	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{4}$	$\frac{1}{2}$
AaBb	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{2}$	-	$-\frac{1}{2}$	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-	$\frac{1}{4}$	$\frac{1}{2}$
Aabb	$\frac{1}{2}$	-	1	-	-	$\frac{1}{2}$	$\frac{1}{2}$	$-\frac{1}{2}$	-1	$\frac{1}{2}$	-	$\frac{1}{2}$	$-\frac{1}{2}$	-	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	$-\frac{1}{4}$	$\frac{1}{2}$
aaBB	-	1	1	-	-	1	-	-1	-	-	1	-	-1	-	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	-	$\frac{1}{4}$
aaBb	-	$\frac{1}{2}$	1	$\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-1	$-\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-1	$-\frac{1}{2}$	$-\frac{1}{2}$	-	$\frac{1}{2}$	$\frac{1}{2}$	-	$-\frac{1}{4}$	$\frac{1}{2}$
aabb	-	-	1	1	-	-	1	-1	-1	-	-	1	-1	-	$-\frac{1}{2}$	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	-	-	$-\frac{1}{2}$

(b)

$L_1 + L_2 - 2L_3$

a_A	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
ad	-1	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	1
dd	$\frac{1}{2}$	-	$-\frac{1}{2}$	-	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$-\frac{1}{2}$	-	$\frac{1}{2}$

Genotype

AABB

AABb

AAbb

AaBB

AaBb

Aabb

aaBB

aaBb

aabb

For the i :th genotype to be tested, one computes $L_{1i} + L_{2i} - 2 L_{3i}$. The a and d terms cancel out, and the epistatic interaction terms alone remains.

Furthermore, this is true for any number of loci, and is also not confined to digenic interactions. This is so, because for any one row, $L_1 + L_2 = L_3$ for the a_i and d_i terms and is therefore independent of the degree of inbreeding.

This latter condition is of great practical importance in that it let us work with heterozygous and vigorous material. For the seed production and the precision of the yield trials this is very important.

Choice of testers.

It is pointed out by Kearsey and Jinks (1968), that in order to achieve reliable estimates of values especially for additive and dominance effects it is important that the lines are wide selections in the character to be studied.

Let us assume, that the population of lines to be studied is heterogeneous for K loci, and of these K' are different between the L_1 and L_2 testers, with $K' \leq K$.

The system will then, according to Kearsey and Jinks, at least detect epistatic interactions between these K' loci, and the same is true for dominance.

The analysis will thus indicate whether or not dominance and epistatic interactions are components of the genetic architecture, but will not indicate their absolute contribution.

In order that the absolute values of the additive variation are correctly estimated, it is essential that the testers L_1 and L_2 differ for all loci involved, that is $K' = K$.

The latter condition is not easy to achieve, particularly when a number of characters are studied, as in the present case, where we study both yield and quality characteristics of the crop.

This type of analysis should be regarded as a means for showing the kinds of gene action involved rather than supplying estimates of the absolute levels of contribution to the mean value of the different types of variation involved.

In view of this, the present study has been confined to determinate whether or not epistatic interactions exists in significant amounts or not.

b. Materials and Methods.

Materials.

The lines used in the study are the results of a practical breeding program. They are lines that have been retained after production of very many lines from many different source materials, and that after repeated and thorough testing have been considered as superior breeding lines.

The testing procedures have included both evaluation of the inbred lines per se, and as components in hybrids. At each stage, only the best material has been considered for further testing.

Thus, the material is very far from randomly chosen, but rather typical of material in an advanced stage of a breeding programme.

The characteristics and origins of the material is as follows :

The tester lines :

Line 1 : An inbred line in the S_3 generation, originates from an English population. Gives, as component in hybrids, rather high yield , a rather high sugar content and rather low values for the impurities K^+ , Na^+ and α - amino N.

Line 2 : An inbred line in the S_3 generation, which originates also from an English population, but a different one than line 1. As component in hybrids it gives very high yield, somewhat low sugar content, and medium levels of K^+ , Na^+ and α - amino N.

Line 3 : An inbred line in the S_1 generation originating from a population selected in Sweden. A rather extreme type, giving very high yields, low to very low sugar content and rather high values for K^+ , Na^+ and α - amino N.

Line 4 : An inbred line in the S_2 generation, selected in Sweden from a population of Swedish origin. The line gives rather high yields with medium to low sugar content and has medium levels of K^+ , Na^+ and α amino N.

Line 5 : An inbred line in the S_2 generation selected in Sweden from a Finnish population. A medium type giving medium high yields, medium sugar content and medium levels of K^+ , Na^+ and α -amino N.

Line 6 : An inbred line in the S_2 generation, selected in France from an English population, which in its turn was selectioned from an old Jugoslavian variety. A line with rather high yield and low sugar content. Medium levels of K^+ , Na^+ and α -amino N.

Line 7 : An inbred line in the S_2 generation, selected in France from an old Dutch variety. The line is rather extreme with very high yields, low sugar content, medium levels of K^+ and Na^+ and rather high levels of α - amino N.

The tested lines.

Line 11: An inbred line in the S_4 generation, selected in California, U S A, in the Salinas valley for winter growing. Under Swedish conditions it gives rather low yield, with medium sugar content and high impurities : K^+ and Na^+ are high and especially α -amino N is very high.

Line 12: An inbred line in the S_2 generation selected in Sweden from an English population. The line gives a rather high yield, with a rather high sugar content and medium to low levels of K^+ , Na^+ and α -amino N.

- Line 13: An inbred line in the S_1 generation, selected in Sweden, originating from the same English population as line 12. But differs from line 12 in that it has a lower yield, higher sugar content. Similar levels of the impurities.
- Line 14: An inbred line in the S_3 generation, selected in Sweden from a population of Finnish origin. The line is characterized by medium yield level with a very high sugar content. Medium levels of the impurities.
- Line 15: An inbred line in the S_3 generation, selected in Sweden from the same Finnish population as line 14. Very different in appearance, although it resembles in the analysed characters : Medium high in yield, high in sugar content, and medium low values in the impurities K^+ Na^+ and ∞ - amino N.
- Line 16: This is a subline of line 12 and inbred one step further : A line in the S_3 generation, and with likewise a rather high yield, a rather high sugar content and medium to low levels of the impurities K^+ , Na^+ and ∞ - amino N.

Populations referred to as originating from a certain country or area, must be understood to have a selection history in that area. In contrast to cereals, fodder species and others, the sugarbeet is very young as a crop and originated as little as about 250 years ago. The first beets that can be called sugar beets were selected in Silesia in northern Germany. All sugar beets are descendants from these original sugar beets.

Methods.

The study has comprised two different trial series, from respectively 1973 and 1976.

The series from 1973 consisted of two different F_1 Male Sterile hybrids (F_1 MS) :

F_1 MS	11 x 12
F_1 MS	13 x 14

which were crossed to each of three different tester sets :

Testers	Set 1	Set 2	Set 3
L_1	1	1	2
L_2	2	3	3
L_3	1 x 2	1 x 3	2 x 3

which gives in total six series of sets of material tested. Furthermore, all of these were tested on three different locations in Sweden :

Location 1	Landskrona (Säbyholm)
" 2	Hököpinge
" 3	Köpingebro

In total we thus have 18 sets of analyses.

The trial series from 1976 was smaller and was comprised 1 F_1 MS :

F_1 MS	15 x 16
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which was crossed to each of two different tester sets :

Testers	Set 1	Set 2
L_1	4	6
L_2	5	7
L_3	4 x 5	6 x 7

and the corresponding field trials were laid out in 4 different trials : Two of them in Sweden, one in Holland and one in France.

Location 1 : Landskrona, (Säbyholm) Sweden

" 2 : Hököpinge, Sweden

" 3 : Emmeloord, Holland

" 4 : Roye, France

This gives a total of two sets of material at four locations, that is eight sets of analyses to do.

Field trials technique.

The field trials were sown at normal sowing time in April - May and harvested in October - November, which is also the normal time of harvest of sugar beet crops. The characteristics of the trials are presented in Table 5.2 for 1973 trials, and in Table 5.3 for 1976 trials.

Table 5.2

Characteristics of locations 1973

	<u>Säbyholm</u>	<u>Hököpinge</u>	<u>Köpingebro</u>
Sowing time	27/4	6/5	30/4
Harvest time	5/10	15/11	25/10
Sugar yield Dt/Ha	73.09	78.56	91.36
Sugar %	18.13	19.35	18.39
K + Na M Eq	5.69	5.09	4.30
α - Amino N	30.47	33.40	26.79
(Colorimetric value)			

It should be noted the relative similarity of the three trials in 1973, as regards yield levels and also the quality characters Sugar content %, K + Na and α -amini N.

This is in contrast to the conditions for the 1976 trials, (Table 5.3) where we have considerable differences between the locations :

Table 5.3

Characteristics of locations 1976

	Säby- holm	Hök- pinge	Emme- loord	Roye
Sowing time	29/4	28/4	8/4	9/4
Harvest time	10/11	1/11	25/10	6/10
Sugar yield Dt/Ha	64.48	85.31	138.44	73.06
Sugar %	18.80	17.97	18.46	15.32
K + Na M Eq	4.45	5.63	6.09	6.37
α - Amino N (Colorimetric value)	22.1	32.2	18.0	48.4

The characters that are under consideration are those traditionally of most interest in the sugar beet production and sugar extraction at the sugar factories.

1. Sugar yield, or the quantity of sugar that is produced per unit area. Either expressed as kilograms per plot, as in this study or more often in tons per ha.

2. Sugar percentage, determined by polarimetric methods. A sugar solution being optically active, its concentration can be measured by its ability to turn polarised light. This is done after a digestion with lead acetate and filtration.

3. Sodium and Potassium (K^+ and Na^+) ions are impurities that impede the sugar crystallisation, and thus causes losses. The content in the clarified juice is measured by flame photometers.

4. α amino nitrogen compounds, or free amino acids likewise causes losses in the sugar recovery. The content is measured by colorimetric methods after reaction with a colouring agent.

The trial plots were all 4 row plots with the two center rows harvested, and the two outer rows discarded as protection rows, in order to avoid plot to plot influence and eliminate the competition effects between adjacent trial plots.

The sowing was made by a machine giving a thin, even braird, but not precision planted. After emergence, the stand was hand singled to give an even plant spacing of about 25 cm in the row.

The material under study was, for field trial reasons, included in a much larger group of materials, and laid out according to the Simple Lattice design, in order to have good estimates of field variation and low error terms.

At harvest, a plot consisted of 65 to 75 beets, which were taken to a laboratory, and as a whole washed, weighed, and passed over a saw pulper which yielded a representative sample of brei for the chemical analysis of the characters described above.

The used system of conducting and analysing field trials corresponds to the normal practice in sugar beet breeding as well as official variety evaluation. It must here be especially noted, that it results in plot mean values, representing the average of the 65 - 75 roots in the plot. No estimate of within plot variation or single plant values is obtained.

Table 5.4

Plot characteristics per country and year

	Row length	Plot size in m ²	Number of plants per plot
1973 Sweden	12 m	12 m ²	65 - 75
1976 Sweden	12 m	12 m ²	65 - 75
Holland	10 m	10 m ²	60 - 70
France	10 m	9 m ²	60 - 70

The trials in Holland were conducted with 6 replications, but all others with 4 replications per location.

Calculation of values for epistatic interaction effects.

For line i , let us denote with L_{1i} , L_{2i} and L_{3i} , the crosses of this line with the three testers L_1 , L_2 and L_3 . For each replication the value for $L_{1i} + L_{2i} - 2.L_{3i}$ is computed. The means over the four (or six) replications are calculated. This value is a measure of the epistatic effects, if significantly different from zero.

These values are computed for all lines, for all characters, and on all locations.

Test for significance.

As indicated above, the material was tested, in the field trials with other material in a much larger group, permitting a Simple Lattice design.

The correction terms for the sub-blocks could then not be used in the computation of the epistatic interaction effects.

The variance components in the analysis of variance corresponding to the differences between these sub-blocks could then not be utilized, and in order to arrive at a correct estimate of the error term for the epistatic interactions in this study, the proper error term from the analysis of variance and the variance component from the sub-block differences have been added (Appendix 1).

c) ResultsTests for presence of epistatic interaction effects in 1973.Table 5.5Epistatic interactions with Hybrid 11 x 12Tester 1 + 2

	Sugar Yield Kg /plot	Sugar %	K+Na M Eq	Q-amino N
Säbyholm	-0.206	-0.613 ^x	-0.40	+2.0
Hököpinge	-0.401	+0.705 ^{xx}	-0.04	+2.5
Köpingebro	-0.145	-0.045	+0.10	+6.3 ^{xx}
Mean	-0.251	+0.016	+0.11	+3.6

Tester 1 + 3

Säbyholm	+0.996 ^x	-0.773 ^x	+1.20 ^x	-1.8
Hököpinge	-0.134	-0.228 ^(x)	+0.19	-1.3
Köpingebro	-1.004 ^x	-0.515 ^{xx}	+0.16	+4.5 ^x
Mean	-0.047	-0.505 ^{xxx}	+0.52 ^x	+0.5

Tester 2 + 3

Säbyholm	+0.948 ^x	-0.070	+0.26	+5.5
Hököpinge	+0.668	+0.905 ^{xx(x)}	+0.02	+0.3
Köpingebro	-1.381 ^x	+0.590 ^{xx}	+0.25	+8.3 ^{xx}
Mean	+0.078	+0.475 ^{xxx}	+0.18	+4.7 ^x

Table 5:5 shows the computed values for epistatic interactions effects on the hybrid (11 x 12) tested with the three tester sets : 1 + 2, 1 + 3, and 2 + 3 respectively. The results are given for each of the three different environments, as well as the mean values over the three environments, as such averages over environments are the normal practice in plant breeding and variety evaluation.

The levels of significance, computed as a conventional t-test, are indicated in the conventional way :

5 % probability as	*
1 % "	* *
0.1% "	* * *

Some slight modifications of this are used :

(*) indicates that the 5 % level is almost but not quite attained

* (*) indicates likewise that the 1 % level is almost but not quite attained

.** (*) thus similarly that the 0.1 % level is almost but not quite attained.

The exact levels of significance of all the computed epistatic interaction values, significant or not, can be found in Appendix 1.

Sugar yield

It is evident from table 5:5 that we have greater differences for the tester pairs 1 + 3 and 2 + 3 than with 1 + 2, in that the former two give significant values, more easily than the latter one.

According to the theory this would mean that the number of different loci, K' , is greater for the lines 1 and 3 and 2 and 3 than for 1 and 2. This might be explained by the fact that line 3 is quite different in origin from 1 and 2. Under the conditions of the three used locations and the year 1973 the combinations 1 + 3 and 2 + 3 form more efficient tester-pairs for detecting epistatic interaction effects.

In each case, with testers 1 and 3 and 2 and 3, we have for two of the locations i.e. Säbyholm and Kjöpingebro, significance for epistatic interactions. It is especially noteworthy that the deviations are positive at Säbyholm and negative at Kjöpingebro.

At the third location, Hököpinge no significant epistatic interaction was observed, and with the tester set 1 + 2 no significant epistatic interaction occurred at either trial location.

Sugar content

The three testers can be said to form a gradient of relative sugar percentages : Line 1 with rather high sugar %, line 2 with an intermediate level and line 3 with a comparatively low sugar content.

However, the greater divergence in the pair 1 + 3 does not show more efficiency in detecting epistatic interactions than do the less diverging pairs 1 + 2 and 2 + 3, rather is the contrary true.

As sugar content in field evaluations is a character determined with much lower coefficients of variation than the others, we could more easily detect significant differences for epistatic interactions. With all three tester pairs we could detect epistatic interactions :

Testers 1 + 2 gave significantly negative interactions ($P = 5\%$) at Säbyholm and a positive ($P = 1\%$) at Hököpinge. Köpingsbro was without apparent epistatic interaction .

With tester 1 + 3 we observe significant epistatic interactions ($P = 5\%$ resp. $P = 1\%$) at all three locations, and further all three are negative.

By contrast, testers 2 + 3 gave significant positive ($P = 1\%$ and $P = \text{almost } 0.1\%$) epistatic interactions on the same locations that were significantly negative with the testers 1 + 3.

$K^+ + Na^+$ (Sodium + Potassium ions) content

In this character we observe only one case of epistatic interactions, and with low significance ($P = 5\%$).

The determination of $K^+ + Na^+$ content values are done with less favourable error levels than for sugar content, but not very high error variation. Also the genetic structure must be different for this character compared with that determining, for example, the sugar content.

Amino nitrogen content

On one location we observe positive interaction values ($P = 5\%$ and 1%) for all three tester pairs. But also for this character it must be said that epistatic interactions are largely absent.

Although the error variation is greater in this character than in the others, it must be concluded that epistatic interactions in $\propto$ amino nitrogen content values are largely absent. It must be added also, that the testers are rather different in this character, tester 1 having rather low values, while for tester 3 the values are more elevated. It is not probable that the lack of interactions is the result of too similar testers ($= K'$ not being too small)

Table 5 : 6

Epistatic interaction effects with hybrid
13 x 14

Tester 1 + 2

	Sugar Yield Kg /Plot	Sugar %	K+Na M Eq	α -amino N
Säbyholm	-0.167	-0.185	-1.35 ^{x(x)}	-0.8
Hököpinge	-0.221	-0.030	+0.45	+0.8
Köpingebro	-1.284 ^x	-0.725 ^{xx(x)}	+0.14	+1.5
Mean	-0.557 ^{xx}	-0.313 ^x	-0.25	+0.5

Tester 1 + 3

Säbyholm	-1.593 ^{x(x)}	-1.995 ^{xx}	+0.94 ^x	+10.8 ^{xx}
Hököpinge	-0.701	-0.725 ^{xx}	-0.66 ^x	+4.3
Köpingebro	-0.637	-0.470 ^{xx}	+0.11	+1.0
Mean	-0.977 ^{xxx}	-0.797 ^{xxx}	+0.13	+5.4 ^x

Tester 2 + 3

Säbyholm	+0.038	+0.155	+0.79 ^x	+9.0 ^x
Hököpinge	-0.756	+0.110	+0.26	+4.0
Köpingebro	-0.080	+0.230 ^x	+0.11	+2.5
Mean	-0.266	+0.165	+0.39	+5.2 ^x

The hybrid tested in Table 5:6 is of a type quite different from 11 x 12, tested in Table 5:5.

The hybrid considered here, 13 x 14, is of a type normally referred to as a Z-type. This indicates that it is a relatively low in yielding ability, high in sugar content and favourable or low values for the Sodium, Potassium and α -amino nitrogen contents.

Sugar yield

All three testers indicate low incidence of epistatic interaction effects. In contrast to hybrid 11 x 12, the effects are more regularly of negative sign, and in this case the averages over the locations are more informative, in that they more easily show high degree of significance. The epistatic interaction with testers 1 + 2 is clearly significant and for testers 1 + 3 highly significant. The third tester pair 2 + 3 detected no significant epistatic interactions on either location, and likewise not as average over locations.

Sugar content

For testing epistatic interactions for sugar content the three tester sets are clearly different. Testers 1 + 2 show highly significant ($P = \text{almost } 0.1 \%$) on one location (Köpingebro) and the other two non-significant. Testers 1 + 3 show significance ($P = 1 \%$) on the same level on all three locations.

Being based on unidirectional interaction effects, the mean over location becomes highly significant ($P < 0.1\%$). The third tester pair 2 + 3 is giving essentially non-significant values for epistatic interactions.

Sodium + Potassium (K^+ + Na^+) content

We observe for K + Na content the same low incidence of significant values for epistatic interactions, as we have observed for the cross 11 x 12 above. In a few cases we observe on single location significance of a lower degree ($P = 5\%$), but due to different reactions in different locations the mean over locations shows no epistatic interaction effects.

Amino nitrogen content

Epistatic interaction values are positive but significant only in two cases. That is largely the same result as for the cross 11 x 12 : epistatic interactions are mainly absent.

Test for presence of epistatic
interaction effects in 1976

Table 5 : 7

Epistatic interaction effects with
hybrid 15 x 16

Tester 4 + 5

	Sugar Yield Kg /Plot	Sugar %	K+Na M Eq	α -amino N
Säbyholm (Sw)	+0.109	+0.615 ^{x(x)}	+0.173	+3.00
Hököpinge(Sw)	-0.838	-0.238	-0.195	+9.25
Emmeloord(Hol)	-0.041	-0.252	+0.253	+4.00 ^x
Roye (Fr)	-0.327	-0.123	+0.160	+7.50

Tester 6 + 7

Säbyholm (Sw)	-0.854 ^(x)	+0.125	+0.833 ^{xx}	+2.75
Hököpinge(Sw)	-0.651	-0.393	+0.263	+8.00
Emmeloord(Hol)	+0.212	-0.847 ^{xxx}	-0.130	+1.67
Roye (Fr)	+0.144	-0.273	+0.485	-2.25

We can observe from Table 5:7, that in spite of our efforts to place the material on different locations with quite different yield levels, as indicated in Table 5:3, which presumably should result in equally widely different environments, we observe rather few cases of significant epistatic interaction effects.

In this context we have to notice the general growing conditions of the trials. 1976 was an extremely hot and dry year for European conditions. This has supposedly given more similar conditions in the experimental environment than intended.

Sugar Yield

For sugar yield we observe only one case of significant ($P = 5\%$) epistatic interaction effects : with testers 6 + 7 on the Säbyholm location. All others have the estimated values below the level of error variation, and thus epistatic interaction effects presumably do not exist.

Sugar content

Sugar content shows significant epistatic interactions in two cases. With testers 4 + 5 it is significant ($P = \text{about } 1\%$) at Säbyholm, and with tester 6 + 7 at Emmeloord in the North East Polder of Holland ($P < 0.1\%$). All other trials were non-significant.

Sodium and Potassium ion content

Only one case of significance ($P = 1 \%$) is recorded with testers 6 + 7, in the Sabyholm trial for the Sodium + Potassium content.

 α - amino nitrogen content

The amino-N content shows still lower incidence of significant epistatic values than the K + Na character. Only one case of low significance exists ($P = 5 \%$ with testers 4 + 5 at Emmeloord in Holland). All other values are below the error level.

d. Discussion

Comparison of the different data sets to estimate the epistatic interaction effects reveal several facts which we can state as follows :

1. Epistatic interactions exist in sugar beet, in all four of the investigated characters.
2. The epistatic interactions can be of different sign on different locations, in that they sometimes raise the yield to a higher level than would be expected with the purely additive-dominance model (positive effect), and sometimes the opposite is true (negative effect).
3. The epistatic interaction between loci evidently also interacts with the year factor (G x Y interaction) in that for the first year (1973) epistatic interactions were rather common and significant, but for the third year (1976) they were largely absent.
4. Different characters seem to be affected to a different degree by the epistatic interactions. The sugar yield and the sugar content seem to be more affected by epistatic interaction than do the quality characters, Sodium and Potassium ion content and the α -amino nitrogen content.

The above statements have, as a consequence, that models which are based on only additive and dominance gene effects run the risk of being too simplified and thus misleading.

This must be regarded as the case at least when dealing with highly selected populations, as the present population of a number of lines from which we intend to construct hybrid varieties.

The combination of epistatic interaction effects between different loci and their interaction with the environment is no new or unexpected complication. On the contrary, genes always do interact with the environment to a lesser or greater degree, and their own interactions must thus also be influenced more or less by the environment. Principally, this must be of the same nature as all genotype x environment interactions.

A somewhat intriguing point is the observation that we observed considerably more significant epistatic interaction values in 1973 than in 1976, although the locations and their characteristics were much more varied in the latter case than in the former.

Possibly the extreme year 1976 caused higher error variation due to drought effects, which then renders the same level of gene effects, to be non-significant. Gene action supposedly is different in different environments. Under the abnormally hot and dry conditions, the growing conditions resembled what is normally mediterranean conditions, and, as it seems, similarly in all the four locations. This would give a similar reaction in all four locations, and in our case epistatic interactions largely absent. Thus the result can partly be explained by an environment interaction effect.

The estimates of the genetic effects depend on the number of loci which differ between the two testers. If the number of these loci is less than that of all loci in the population for the trait, we will have underestimates of the genetic effects. As we have practically no significant epistatic interaction values, this could indicate that we have few loci segregating in the material in the 1976 years study.

A third possibility is that the segregating loci only rarely show epistatic interactions.

6. Experiment II

A scaling test to estimate genetic parameters.

a) Introduction

The scaling test is a procedure which allows the separation and estimation of gene effects involved in the inheritance of quantitative traits. Estimate of additive, dominance, additive x additive, additive x dominance and dominance x dominance gene effects are obtained. A comparison of these estimates indicates the relative importance of the gene effects in the inheritance of a quantitative trait.

The test uses two inbred lines P_1 and P_2 and crosses and backcrosses produced from them : P_1 , P_2 , F_1 , F_2 , P_1F_1 and P_2F_1 .

Presence of epistatic interactions are inferred from the failure to observe the relationships between generation means that are expected on an additive-dominance model (Mather and Jinks 1982).

The introduction of test of generation means was introduced by Mather (1949) to detect epistatic interaction effects.

The test was developed by several persons, i.e. Cavalli (1952), Anderson and Kempthorne (1954), Jinks (1956) and Hayman (1957). But in particular, Anderson and Kempthorne showed that all the information about additive dominance and digenic epistatic

interaction variation available in the means of generations descended from two inbred lines is contained in just six parameters.

We assume, in analogy with Experiment I, that in the source material there exists genetic variation within K loci, and the two inbred lines differ from each other in K' of these, where $K' \leq K$. If K' is small this means that the gene effects will be underestimated, since homology, and thus no contribution to the value of the estimates, exists for several loci.

The test must thus be regarded as a positive test : presence of significant epistatic interactions is a proof of their existence, but a negative result is thus not a proof of their absence.

b) Materials and Methods

Materials

Three inbred lines, 21, 22 and 23 from the monogerm back crossing programme have been used in the study. The level of inbreeding was S_5 , S_6 and S_5 respectively.

The lines were so called 0-types, which means that they are maintainer-types of cytoplasmically male sterile (CMS) lines. The male sterile line has always been reproduced together with its maintainer line during development and reproduction, which has permitted to have each genotype, in two different versions : a male sterile form and a male fertile form, depending on the type of cytoplasm (S-or N-cytoplasm).

In order to have male fertile F_1 hybrids for production of back-crosses, an initial F_1 hybrid was made with help of a marker gene : red coloured hypocotyl., the red colour being dominant over the green colour. True F_1 hybrids could thus be selected in the population grown from seed harvested on the green hypocotyl plants.

In order to have a uniform seed quality for the field trials, all the necessary generations were produced with the aid of the MS-equivalents, and the F_2 and Back-cross generations were produced in the same area, in the year preceding the field test. The seed growing conditions are in sugar beets known to greatly influence the outcome of field tests,

so this procedure was necessary in order to minimize as much as possible unwanted influences on the results.

Description of the lines

The characteristic of the inbred lines per se are presented in Table 6 : 2.

Table 6 : 2

Characteristics of the lines used in Experiment II.

Line	Root Yield dt/ha	Sugar %	Sugar Yield dt/ha	K ⁺ content meq	Na ⁺ content meq	α-amino N content col.value
21	319.6	13.40	45.96	3.76	4.46	22
22	158.8	15.86	27.51	3.95	1.43	52
23	158.7	16.99	28.93	3.97	1.04	33

Line 21 : Has a rather big root yield and low sugar content, compared with the two other lines. It has also a high Sodium (Na⁺) level and a low value for α-amino nitrogen content.

Line 22 : This line has a rather low root yield with a medium sugar content, medium sodium content level, but a very high content of α-amino nitrogen.

Line 23 : The highest sugar content with a rather low root yield are combined. The line also has the lowest sodium content and medium α-amino nitrogen.

It must also be noted that for the Potassium (K⁺) content all three lines have similar values.

Methods

The three lines were combined in the three possible combinations :

21 x 22

21 x 23

22 x 23

and, as indicated above, in the year that preceded the field test, the following generations were produced (1973)

P_1 seed multiplication of the O-type P_1

P_2 seed multiplication of the O-type P_2

F_1 cross between the MS equivalent of P_1 and the O-type P_2

F_2 the fertile F_1 reproduced to produce the F_2 generation

$P_1 F_1$ the MS equivalent of P_1 crossed with the fertile F_1 hybrid $P_1 \times P_2$

$P_2 F_1$ the MS equivalent of P_2 crossed with the fertile F_1 hybrid $P_1 \times P_2$

This constitutes the six generations that are needed to estimate the additive, dominance and digenic epistatic interaction effects.

The field test was carried out with 8 replications on one location : Köpingsbro. The field plots were 4 row plots, with the center two rows harvested. Outer rows were regarded as protection rows, to protect against unwanted inter-plot competition effects, and discarded.

The number of plants per plot was about 60 to 65, giving about 500 plants per generation as the total number of plants in the 8 replications.

The field trial characteristics are as follows :

Year : 1974

Location : Köpingsbro, Sweden

Statistical design : Randomized blocks

Plot size : 4 rows, 8 meters

Harvested plot : The two center rows

Plant number per plot : 60 - 65

Row distance : 45 centimeters

Number of replications : 8

Sowing date : 19 april

Harvest period : 1 - 16 october

Analysis of variance

Analysis of variance has been performed for all characters in the study, according to the form presented in Table 6 : 3. The values for Sodium and Potassium were summed, according to the standard procedures, as their effects are very similar in the sugar extraction process.

Table 6 : 3

Form of analysis of variance for the
Experiment II study

Source of variation	Degrees of freedom	Mean square	Expected mean squares
Varieties	$v - 1$	ms 1	$\sigma^2_e + \sigma^2_v$
Replications	$r - 1$	ms 2	$\sigma^2_e + \sigma^2_r$
Pooled error	$(r-1)(v-1)$	ms 3	σ^2_e
Total	$r \cdot v - 1$		$\sigma^2_e + \sigma^2_r + \sigma^2_v$

The individual analysis of variance for the different characters are presented in Appendix 5

Calculation of genetic effects

When no epistatic interactions are present, the expectations of the following quantities are zero, but in presence of such epistatic interactions each type of test depends on characteristic combinations for its departure from zero. We can calculate the following quantities :

$$\begin{aligned}
 a &= P_1 F_1 - P_2 F_1 \\
 d &= -\frac{1}{2} P_1 - \frac{1}{2} P_2 + F_1 - 4 F_2 + 2 P_1 F_1 + 2 P_2 F_1 \\
 aa &= -4 F_2 + 2 P_1 F_1 + 2 P_2 F_1 \\
 ad &= -\frac{1}{2} P_1 + \frac{1}{2} P_2 + P_1 F_1 - P_2 F_1 \\
 dd &= P_1 + P_2 + 2 F_1 + 4 F_2 - 4 P_1 F_1 - 4 P_2 F_1
 \end{aligned}$$

where

a = additive gene effects

d = dominance gene effects

aa = additive x additive interactions effects

ad = additive x dominance interaction effects

dd = dominance x dominance interaction effects

These denominations follow that of Gamble (1962 a and 1962 b)

The expected generation mean values, are also given by Gamble (1962 a) :

$$P_1 = m + a - \frac{1}{2} d + aa - ad + \frac{1}{4} dd$$

$$P_2 = m - a - \frac{1}{2} d + aa + ad + \frac{1}{4} dd$$

$$F_1 = m + \frac{1}{2} d + \frac{1}{4} dd$$

$$F_2 = m$$

$$P_1 F_1 = m + \frac{1}{2} a + \frac{1}{4} aa$$

$$P_2 F_1 = m - \frac{1}{2} a + \frac{1}{4} aa$$

where m = the mean effect, and a, d, aa, ad and dd as defined above.

The error terms for the calculated genetic effects are estimated from the error term σ^2_e in the analysis of variance.

Since the field trial procedure did not permit plant to plant analysis within the plot, and thus whole plot analysis was performed, the analysis of variance gives the best estimate of the error.

The error terms are thus for

$$m = \sqrt{\sigma^2}$$

$$a = \sqrt{2 \cdot \sigma^2}$$

$$d = \sqrt{10 \cdot \sigma^2}$$

$$aa = \sqrt{8 \cdot \sigma^2}$$

$$ad = \sqrt{3 \cdot \sigma^2}$$

$$dd = \sqrt{16 \cdot \sigma^2}$$

Conventional significance levels are indicated :

-	Non significant
*	Significant at the 5 % level
* *	Significant at the 1 % level
* * *	Significant at the 0,1 % level

C.ResultsTable 6 : 4

Mean performance of parents and crosses
for six characters.

Cross 21 x 22

Generation	Root yield dt/ha	Sugar %	Sugar yield dt/ha	K ⁺ content meq	Na ⁺ content meq	Amino-N content col.value
P ₁	319.6	13.40	45.76	3.76	4.46	22.0
P ₂	158.8	15.86	27.51	3.95	1.43	52.0
F ₁	490.3	16.06	77.18	3.78	2.49	21.0
F ₂	414.0	15.59	64.01	3.47	2.75	23.0
P ₁ F ₁	435.3	15.56	66.28	3.60	2.95	20.0
P ₂ F ₁	347.7	15.94	54.68	3.48	2.48	27.0

Table 6 : 4 shows the mean performance over the eight replications of the six different characters for the six parents and cross generations, for the cross 21 x 22.

Similarly Table 6 : 5 shows the mean performances of the cross 21 x 23 and Table 6 : 6 the mean performances of the cross 22 x 23.

Table 6 : 5

Mean performance of parents and crosses for six characters.

Cross 21 x 23

Generation	Root yield dt/ha	Sugar %	Sugar yield dt/ha	K ⁺ cont. meq	Na ⁺ cont. meq	Amino- N cont. col.value
P ₁	319.6	13.40	45.76	3.76	4.46	22.0
P ₂	158.7	16.99	28.93	3.97	1.04	33.0
F ₁	424.0	16.35	68.94	3.97	2.07	21.0
F ₂	366.6	16.41	60.10	3.94	1.90	25.0
P ₁ F ₁	419.6	15.87	65.93	3.80	2.46	21.0
P ₂ F ₁	334.8	16.78	55.92	3.90	1.32	27.0

Table 6 : 6

Mean performance of parents and crosses
for six characters.

Cross 22 x 23

Generation	Root yield dt/ha	Sugar %	Sugar yield dt/ha	K ⁺ cont. meq	Na ⁺ cont. meq	Amino-N cont. col.value
P ₁	158.8	15.86	27.51	3.95	1.43	52.0
P ₂	158.7	16.99	28.93	3.97	1.04	33.0
F ₁	351.2	17.75	62.47	3.68	1.02	29.0
F ₂	171.6	16.34	28.24	3.86	1.27	45.0
P ₁ F ₁	180.7	16.70	30.10	3.74	1.49	40.0
P ₂ F ₁	345.0	17.82	60.58	3.73	0.92	26.0

The P₂F₁ generation is perhaps more deviating than expected, and resembles that of the F₁. Errors due to accidents or mistakes in the handling of seed and plant material can not be absolutely excluded, but based on experience such errors are rare. If we assume, for example, that P₂F₁ would instead resemble P₁F₁, we would still observe epistatic interactions. In this case we obtain higher values for the d effects and aa instead of dd interactions.

The 21 x 22 crossTable 6 : 7

Estimates of gene effects

	Root yield dt/ha	Sugar %	Sugar yield dt/ha	K ⁺ content	Na ⁺ content	Amino - N content col.value
m	414.0	15.59	64.01	3.47	2.75	23.0
a	+ 87.6 ⁻	- 0.38 ⁻	+ 11.60 ⁻	+ 0.12 ⁻	+ 0.47 ⁻	- 7.0 ⁻
d	+ 161.1 ⁻	+ 2.07 ⁻	+ 26.43 ⁻	+ 0.20 ⁻	- 0.60 ⁻	- 14.0 ⁻
aa	- 90.0 ⁻	+ 0.64 ⁻	- 14.12 ⁻	+ 0.28 ⁻	- 0.14 ⁻	+ 2.0 ⁻
ad	+ 7.2 ⁻	+ 0.85 ⁻	+ 2.47 ⁻	+ 0.22 ⁻	- 1.04 [*]	+ 8.0 ⁻
dd	- 17.0 ⁻	- 2.26 ⁻	- 0.17 ⁻	+ 0.83 ⁻	+ 0.15 ⁻	+ 20.0 ⁻

In the 21 x 22 cross none of the estimated gene effects are significant, except for a low level of significance (5 %) for the ad interaction value for Sodium content. This means that epistatic interactions were either absent or present in only small amounts.

The 21 x 23 crossTable 6 : 8

Estimates of gene effects

	Root yield dt/ha	Sugar %	Sugar yield dt/ha	K ⁺ content	Na ⁺ content	Amino-N content col.value
m	366.60	16.41	60.10	3.94	1.90	25.0
a	+ 84.80 ⁻	- 0.91 ⁻	+ 10.01 ⁻	- 0.10 ⁻	+ 1.14 ^{**}	- 6.0 ⁻
d	+ 227.25 [*]	+ 0.81 ⁻	+ 34.89 ⁻	- 0.26 ⁻	- 0.72 ⁻	-10.5 ⁻
aa	+ 42.40 ⁻	- 0.34 ⁻	+ 3.30 ⁻	- 0.36 ⁻	- 0.04 ⁻	- 4.0 ⁻
ad	+ 4.35 ⁻	+ 0.89 ⁻	+ 1.60 ⁻	+ 0.10 ⁻	- 0.57 ⁻	- 0.5 ⁻
dd	- 224.90 ⁻	- 1.87 ⁻	+ 65.57 ^{**}	+ 0.63 ⁻	+ 2.12 [*]	+ 5.0 ⁻

The outcome of the cross 21 x 23 is slightly more favourable for the detection of epistatic interactions. We have significant dd interactions for sugar yield and sodium (Na⁺) content. Significant are also the additive effects for sodium content, and the dominance effects for root yield.

Noteworthy is perhaps the presence of both relatively high amounts of dominance effects for root yield and epistatic dd deviations for sugar yield.

The 22 x 23 crossTable 6 : 9

Estimates of gene effects

	Root weight	Sugar %	Sugar yield dt/ha	K ⁺ content	Na ⁺ content	Amino-N content col.value
m	171.6	16.34	28.24	3.86	1.27	45.0
a	+ 164.3 ^{**}	- 1.12 ⁻	- 30.48 ^{**}	+ 0.01 ⁻	+ 0.57 ⁻	+ 14.0 [*]
d	+ 557.5 ^{*(*)}	+ 5.00 ^{**}	+102.65 ^{***}	- 0.79 ⁻	- 0.48 ⁻	- 61.5 ^{**}
aa	+ 365.0 ^{**}	+ 3.68 ^{**}	+ 68.40 ^{**}	- 0.50 ⁻	- 0.26 ⁻	- 48.0 ^{**}
ad	- 164.4 [*]	- 0.55 ⁻	- 29.76 [*]	+ 0.02 ⁻	+ 0.37 ⁻	+ 4.5 ⁻
dd	- 396.5 [*]	- 4.37 [*]	- 68.38 [*]	+ 0.84 ⁻	- 0.05 ⁻	+ 59.0 ^{**}

The 22 x 23 Cross has given considerable more effects of all three kinds of digenic epistatic deviations.

For root weight we observe significant positive deviations for the aa effects (+ 365.0 dt/ha) and almost significant negative values for the ad (- 164.4 dt/ha) and dd effects (+ 557.5).

Also the first degree effects, the additive (a) component is significant (+ 164.3) as well as the dominance effects (+ 557.5).

The sugar content also shows significant gene effects, in that the d-component (+ 5.00 % sugar),

the aa-component (+ 3.68 % sugar) and the dd-component (- 4.37 %) are significant, while the a and the ad component remains insignificant.

Sugar yield shows all genetic effects significant with significance on different levels. Of the epistatic effects are the aa significant and ad and dd almost significant with respectively + 68.40 dt/ha, - 29.76 dt/ha and - 68.38 dt/ha. Highly significant are the dominance effects (+ 102.65) and significant are also the additive components (- 30.48 dt/ha).

Of the quality characters, K^+ ion content and Na^+ ion content show no significant gene effects. By contrast, the gene effects for amino nitrogen are significant : aa and dd effects are both significant with the values - 48.0 and + 59.0 respectively and the d-effects (- 61.5) and the a effects (+ 14.0) also significant. Only the ad effects remains non-significant.

It should be noted that for root yield the sign for first degree relationships, the a and the d effects, are all of positive sign, although not all of them are significant, while the second degree relationships, i.e. the epistatic aa, ad and dd deviations, are variable both within and between crosses.

Of course, two parameters will change sign if we change which parent is considered P_1 respectively P_2 : The a and the ad parameters will change with the change of order of the parents.

As arranged here, the better parent in root yield was considered P_1 , and this then gives constantly positive estimates for a and d gene effects. Other parameters would remain unaffected.

The same will be true when observing the sugar yield with always P_1 as the higher yielding parent. (This requires a change for the 22 x 23 cross).

For the sugar content this observation is no longer true. We would have in some cases positive values and in some cases negative values.

For the quality characters the outcome of a change of P_1 and P_2 would be variable.

Relative amounts of gene effects

For a consideration of the epistatic interaction effects compared with the additive and dominance effects, the aa, ad and dd effects may be summed together in their absolute values in order to illustrate their importance.

The gene effects for sugar yield are thus summed and presented in Table 6 : 10 both with their absolute values and relative proportions of genetic effects.

Table 6 : 10

Summary of gene effects

Sugar Yield

Absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	11.60 ⁻	10.01 ⁻	30.48 ^{**}
Dominance	26.43 ⁻	34.89 ⁻	102.65 ^{***}
Epistatic	16.76 ⁻	70.47 [*]	166.54 ^{***}

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	21.2 %	8.7 %	10.2 %
Dominance	48.2 %	30.2 %	34.3 %
Epistatic	30.6 %	61.1 %	55.6 %

From this table it is evident that the levels of detected genetic effects are very different in the three different crossings. The 22 x 23 cross shows much greater values than 21 x 23 and especially 21 x 22. Reasonably this means that the number of gene differences K' is greater between 22 and 23, than between 21 and 23. 21 and 22 should then have few genes that are different between the two lines.

From the relative proportions we can see that the relative amounts of additive, dominance and epistatic interaction effects are rather similar, in spite of the dramatic differences in absolute levels.

For the sugar content the genetic effects are presented in table 6 : 11.

Table 6 : 11

Summary of genetic effects

Sugar content

absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	0.38 ⁻	0.91 ⁻	1.12 ⁻
Dominance	2.07 ⁻	0.81 ⁻	5.00 ^{**}
Epistatic	3.75 ⁻	3.10 ⁻	8.60 ^{**}

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	6.1 %	18.9 %	7.6 %
Dominance	33.4 %	16.8 %	34.0 %
Epistatic	60.5 %	64.3 %	58.4 %

For the first two crosses, none of the genetic effects are significant. Only the cross 22 x 23 shows significance, and we can observe, like for sugar yield that the absolute values are low for the crosses 21 x 22, 21 x 23, and considerably higher for 22 x 23. The relative proportions of the types of genetic effects remain, however, rather constant.

Table 6 : 12

Summary of genetic effects

Root yield

Absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	87.6 ⁻	84.8 ⁻	164.3 ^{**}
Dominance	161.1 ⁻	227.3 ^(*)	557.5 ^{*(*)}
Epistatic	114.2 ⁻	271.7 ⁻	925.9 [*]

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	24.1 %	14.5 %	10.0 %
Dominance	44.4 %	38.9 %	33.8 %
Epistatic	31.5 %	46.5 %	56.2 %

Less pronounced, the results for root yield resemble that of sugar yield and sugar content : The cross 21 x 22 is entirely non significant, while the cross 21 x 23 has a value of $P = 5 \%$ for dominance effects. The cross 22 x 23 shows significant differences for additive ($P < 1 \%$) and dominance genetic effects ($P = 1 \%$). The epistatic interaction effects exist, but on a lower level ($P < 5 \%$).

The relative proportions of genetic effects remain rather constant among the crosses, in spite of quite different levels of absolute values. This, again, is parallel to what we see for sugar yield and sugar content.

Table 6 : 13

Summary of genetic effects

Potassium ion (K^+) content

Absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	0.12 ⁻	0.10 ⁻	0.01 ⁻
Dominance	0.20 ⁻	0.26 ⁻	0.79 ⁻
Epistatic	1.33 ⁻	1.00 ⁻	1.36 ⁻

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	7.3 %	7.4 %	0.5 %
Dominance	12.1 %	19.1 %	36.6 %
Epistatic	80.6 %	73.5 %	62.9 %

All values for types of genetic effects are non significant for K^+ ion content.

The sodium ion content differs from the yield characters in that most of the genetic effects encountered corresponds to additive genetic effects, for which we have significance in all three crosses. The only other significance is for dd epistatic interaction effects in the cross 21 x 23. Also, in contrast to the yield factors, the absolute values of estimated effects seem more or less equal between the crosses.

Table 6 : 14

Summary of genetic effects

Sodium ion (Na^+) content

Absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	0.47 [*]	1.14 ^{***}	0.57 [*]
Dominance	0.60 ⁻	0.72 ⁻	0.48 ⁻
Epistatic	1.33 ⁻	2.73 ^{**}	0.68 ⁻

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	19.6 %	24.8 %	32.9 %
Dominance	25.0 %	15.7 %	27.7 %
Epistatic	55.4 %	59.5 %	39.3 %

Table 6 : 15

Summary of genetic effects

α - amino-nitrogen content, measured
by a colorimetric value.

Absolute values :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	7.0 ⁻	6.0 ⁻	14.0 [*]
Dominance	14.0 ⁻	10.5 ⁻	61.5 ^{**(*)}
Epistatic	30.0 ⁻	9.5 ⁻	111.5 ^{***}

Expressed as relative proportions :

Type of variation	<u>Cross</u>		
	21 x 22	21 x 23	22 x 23
Additive	13.7 %	23.1 %	7.5 %
Dominance	27.5 %	40.4 %	32.9 %
Epistatic	58.8 %	36.5 %	59.6 %

For the α - amino nitrogen content the first two crosses, 21 x 22 and 21 x 23 are without significant genetic effects, the third, 22 x 23, shows significance for all three types of gene effects, especially epistatic interaction shows a high degree of significance. Furthermore, the absolute values for the third cross are very much higher than for the other two crosses.

d. Discussion

It is evident from the results that epistatic interactions exist in sugar beet, and for all the characters that are of importance for the agriculture or the technological use. On the other hand, all combinations of genotypes do not show epistatic interaction effects. This means reasonably, that the number of gene differences K' , that was indicated in the introductory parts, must in fact be rather low.

The big differences between line 21 and the two others, 22 and 23, in the lines own performance regarding the yield factors root yield, sugar percentage and sugar yield are not reflected in significant estimation of gene effects. The performances of the generations from the crosses 21 x 22 and 21 x 23, as shown in Tables 6 : 7 and 6 : 8, are sufficiently well represented by the overall generation mean m . Additive, dominance and digenic epistatic interaction effects give only small contributions, or none at all.

In the third cross the value for the overall mean (Table 6 : 9) is considerably lower, and can not alone represent the value of the generations. Additive effects are significant, and especially so the dominance effects. Of the epistatic interactions the interactions between additive loci are most important.

For all three yield characters we have a high level of significance ($P < 1\%$). The ad and dd interactions are less significant ($P < 5\%$) but clearly present.

For the quality characters, sodium (Na^+), potassium (K^+), and α - amino-nitrogen contents, we seem to find less significant genetic effects than with the yield characters. This concerns both the additive and dominance effect estimations and the three kinds of epistatic interaction estimations, as is shown particularly in Table 6 : 9. The situation is also clearly different between the salt ion concentrations and the amino-nitrogen content. For the potassium values this is easily understandable, as we had high similarity between the lines (Table 6 : 2) and the resulting absence of significance for genetic effects reasonably means that we had no genetic difference between the lines. That is, the number of loci with gene differences K' is 0 or close to 0.

For sodium content, line 21 is obviously deviating from the other two (Table 6 : 2) and this could be expected to result in significant genetic effects, perhaps of all three kinds, in the crosses 21 x 22 and 21 x 23. These two crosses behave in fact very different.

The 21 x 22 cross has the four generations resulting from crossings of very similar value more or less at the mid-parent value. (Table 6 : 4). Probably, this indicates a more complex situation than can be analysed by a digenic interaction system.

The 21 x 23 cross is different (Table 6 : 5), and in the analysis (Table 6 : 8) we observe highly significant values for additive gene effects. The epistatic interactions are of the dd type.

From the 22 x 23 cross it is noteworthy that we have only additive effects present significantly.

The amino nitrogen content behaves perhaps somewhat differently from the other two quality characteristics. But also in this case the cross between the most extreme lines, 21 and 22 have yielded generations with very similar values (Table 6 : 4) which in turn has resulted in small insignificant values (Table 6 : 7) for genetic effects.

It might be suspected for the parent P_2 value that it could be over-estimated. When investigating the other cross, where 22 is a component, it is clear, however, that this is not so. In Table 6 : 6, where line 22 is parent P_1 , it is clear that we get very decisive genetic effects. These result in significant estimates for both additive, dominance and epistatic interaction effects. (Table 6 : 9). The latter are of aa and dd type, with ad completely lacking.

Taken together, these two crosses tell us that the amino nitrogen content is determined by rather complex genetic systems, which evidently comprise more complex interactions than do digenic ones.

The third cross, 21 x 23, where the two parental lines are similar, has given no significant estimates of genetic effects. Thus we have most probably fixed the same genes in the two lines. (Table 6 : 5 and Table 6 : 8.)

In the selection history measures for root yield and sugar percentage have been made since the beginning of selection in sugar beet. One might therefore expect that especially the additive variation, but also to some extent the dominance variation, could largely have been made use of and little useful genetic variation remaining for selection. A larger proportion of the genetic variation would then consist of epistatic interactions.

The contrary might be expected for the quality characters, which have a much shorter selection history because of lack of necessary analysis equipment in the early days. These expectancies would parallel the findings of Stuber and Moll (1971), referred to earlier, who found higher values for estimates of epistatic interaction from selected than from unselected material.

The expected observations do not quite hold for the investigated material, although there is a hint that the additive gene effects are larger for some quality measures. The explanation for this lack of conformity with the expectations is at least twofold :

1. The lines are only three, and pure coincidence might make the results deviating from the expectation.
2. The lines are not randomly chosen. On the contrary, they have been retained after repeated testing, observation and test crossing. Also the quality characters have been severely selected for.

A third observation can also be made : Robinson et al (1949 and 1955) have obtained results which indicate that additive genetic variation is greater in those attributes suspected of having a less complex inheritance. At least the amino nitrogen content must have a very complex inheritance, since the amino acids are intimately involved in all the plant cell activities, and thus reasonably depends on many genes.

7. General discussion

High yield and good quality are the important end results of sugar beet breeding. In combining the genes to form a superior genotype, one must consider the genetic structure, and especially the types of gene action involved.

On the basis of the rather limited material in this study, epistatic interaction effects often contribute significantly to the inheritance of quantitative attributes in sugar beet, besides the additive and dominance types of gene effects.

The epistatic interaction effects seem also to be relatively important, in that our estimates of their relative importance (Tables 6 : 10-15) elevates to around 50 % of the total genetic effects. This underlines the importance of considering these interactions when choosing breeding methods and the type of hybrids to be produced.

Several geneticists, like both Fisher and Mather, have regarded the epistatic interactions as an important factor, if not the major one, in heterosis and inbreeding depression. This view is still very much held today, and has been formed to a linkage-theory by Demarly (1977). According to this theory the epistatic interactions induce the formation of combination of genes where interactions are favourable, and these linkage groups are protected by mechanisms evolved together with the formation of these groups.

Such linkage groups, formed by repeated selections, would then be expected to be more pronounced in highly selected traits or populations and less pronounced in less selected material (Rives, 1984). Stuber and Moll (1971) made a study where they, from a population of maize produced inbred lines carefully chosen after test cross performance, and also inbreds produced at random. In the former case they found more often epistatic interactions than in the latter.

This investigation would indicate the same relationship, although a comparison with randomly chosen inbreds was not possible to do.

Interesting new light upon the question of heterosis and gene action is shed by the molecular genetic studies. Especially the question of gene regulation and the coordination of the great number of genes to produce the phenotype. These regulatory genes control the time and level of expression of the structural genes. Further, for one structural gene there exist several regulatory genes, often one in an adjacent position and several others at distance (Korockstein 1978, Parigen 1979, and Scandalios and Baum 1982). One regulatory gene also controls several structural genes. All these findings show that the gene regulation should rather be seen as a network and not as distinct pathways.

These regulatory genes have been found to be very polymorphic. Klose (1982) has estimated, in mouse, that up to 90 % of the genetic variability could be attributed to the regulatory genes.

Zivy et al (1983) have shown that about 50 % of the genetic differences in the wheat varieties Chinese Spring and Selkirk concerned the regulatory genes.

Considering the knowledge cited above, it is interesting that in this study we find around 50 % of the estimated gene effects to depend on epistatic interactions.

When regulatory genes regulate more than one structural gene, and measuring the effect of these structural genes as metric measurements on the phenotype, we should observe as interaction effects what is in reality variation on the regulatory level. This study being no proof of the relationship between regulatory gene variation and phenotypically observed epistatic interaction effects, it is all the same a very interesting parallel.

High levels of non-additive variance have been found for root yield by Hecker (1967), who after analysis of polycross progeny lines found additive genetic variance to be 0.000976 and the non-additive genetic variance 0.017037. That is, the non-additive variance was 17.5 times greater than the additive. This is in good agreement with the findings in this study.

For sugar percentage Hecker found about equal values for additive (0.6165) and non-additive (0.5973) variance.

Interesting is also a study by Le Cochec and Soreau (1982), who studied general and specific combining ability between sugar beet and fodder beet inbred lines. Since phenotype of fodder beets is very different from the one of sugar beets, one can expect that the main difference lies in genes with mainly additive effects. This is also exactly what Le Cochec and Soreau find, as they estimate GCA and SCA components of variance. GCA was much more important and is genetically composed by additive gene effects and their interactions ($V_A + V_{AA} + V_{AAA} + \dots$). Tests over several years revealed regularly 85-100 % of GCA effects.

These findings rather support the hypothesis that highly selected genotypes contain less additive and more non-additive gene effects. Fodder beets may be regarded as unselected sugar beets, as fodder beets are supposed to be the parental material for all existing sugar beets, eventually after a cross between fodder beets and *Beta maritima*.

Recently Skaracis and Smith (1984) studied three-way top cross hybrid sugar beet performance, and compared the actual yield with several methods of prediction. If we accept an additive-dominance model for genetic effects, we should have good correlations between predicted and real yield values. Presence of epistatic interaction effects would cause a less good correlation.

Skaracis and Smith found for root yield correlations between 0.22 and 0.64 with 5 out of 10 significant.

For sugar content correlations from 0.01 to 0.86 with 5 out of 9 significant. The quality characters were combined to form a purity value, for which they found the correlations to be between 0.02 and 0.77 with 6 out of 10 significant.

These results are interpreted by Skaracis and Smith to indicate that epistatic interactions are largely absent. However, they agree perfectly with the results of this study, which indicate that epistatic interactions are sometimes significantly present (gives low prediction correlations) but often not present. Strictly parallel is also the observation that correlations are higher in 1980 than in 1981. The latter year could then be interpreted to favour epistatic interactions and thus cause lower correlation coefficients.

The study by Skaracis and Smith thus agrees with the results of this study.

Conclusions

For the material used in this study epistatic interactions are present in sufficient magnitude to be important in the inheritance of the agronomically and technologically attributes of sugar beets. They are for highly selected lines often very important, and comprise about half of the genetic variability.

The epistatic interactions show interaction with the environment, and a certain interaction effect (i.e. aa, ad or dd) can sometimes be to the advantage and sometimes to the disadvantage for the performance of the hybrid in question.

It was not the objective of this study to make inferences concerning gene action in sugar beet as a whole, the number of lines in the study being too small for this. It is evident, however, that epistatic interactions exist and breeding procedures and crossing systems for utilizing the selected lines must take these interactions into account.

A breeding system aiming at specific hybrids, so called F_1 varieties, must be conducted in order to make use of the occurring epistatic interactions. Reciprocal recurrent selection should be an efficient method to make use of all kinds of genetic effects.

Summary

The goal of this project has been to examine the genetic mechanisms for the yield and quality characters in sugar beet. Most attention has been paid to the epistatic interactions in the restricted number of lines that is the result of a breeding programme with extensive field testing.

In total the investigation has dealt with 16 inbred lines, studied by two methods : The Triple Test Cross and the Scaling Test.

1. The triple test cross hybrids were field tested in two years and several locations. Epistatic interactions were found in significant amounts in all characters : sugar yield, sugar content, sodium + potassium content and α -amino nitrogen content. The epistatic interaction effects also showed interaction with the environment, so that the effects were significantly different in different environments. Characters with a longer selection history (sugar yield and sugar content) tend to have a higher proportion of the genetic variation as epistatic interaction variation than characters with a shorter selection history (sodium, potassium and amino-nitrogen contents)

2. The scaling test estimates additive, dominance, additive x additive, additive x dominance and dominance x dominance gene effects. All these gene effects were found to contribute to the inheritance of the characters studied : root yield, sugar yield, sugar content,

sodium content, potassium content, potassium content and amino nitrogen content. The overall importance of the epistatic interactions (add. x add., add. x dom. and dom. x dom.) represented about 50 % of the available genetic variance.

The results of this study seem to agree very well with published results on gene action in sugar beets.

3. It was concluded that for efficient breeding programs it is necessary, that epistatic interactions are taken into account, as for example in recurrent selection schemes. Furthermore the study revealed that the epistatic interactions are important to consider when making hybrid varieties from selected inbred lines.

Relationship between the parameters
for gene effects used by different authors.

Gene effect	Johansson, Gamble	Anderson & Kempthorne	Hayman, Jinks, Mathe
Mean	m	K_2	m
Additive	a	$E + F$	d
Dominance	d	$2E$	h
Additive x additive	aa	$G + L + M$	i
Additive x dominance	ad	$2G + L$	j
Dominance x dominance	dd	$+G$	l

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Ressons, France April 1984.

Evert Johansson.

Appendix 1Analysis of variance, 1973

Experiment I

SÄBYHOLMSugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	12.4500	
Sub-blocks	36	17.9584	0.498845
Varieties	99	59.3125	
Error	253	79.6658	0.314884

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	23.6800	
Sub-blocks	36	13.7838	0.382883
Varieties	99	57.4844	
Error	255	16.8643	0.066135

K⁺ + Na⁺ content meq

Source of variation	df	Sums of squares	Mean square
Blocks	3	13.6900	
Sub-blocks	36	18.0155	0.500432
Varieties	99	89.4775	
Error	255	52.5474	0.206068

α-amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	3	3605.7584	
Sub-blocks	36	1826.7440	50.743
Varieties	99	3426.0000	
Error	255	4005.1184	15.706

HÖKÖPINGESugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	34.7400	
Sub-blocks	36	26.4402	0.734451
Varieties	99	33.7813	
Error	260	58.7690	0.226035

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	29.5500	
Sub-blocks	36	5.0819	0.141165
Varieties	99	81.1406	
Error	261	1.5400	0.005900

K⁺ + Na⁺ content meg

Source of variation	df	Sums of squares	Mean square
Blocks	3	1.0750	
Sub-blocks	36	16.6837	0.463437
Varieties	99	50.2061	
Error	261	22.8633	0.087599

 α - amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	3	129.2799	
Sub-blocks	36	946.6245	26.295
Varieties	99	4461.7488	
Error	261	3228.1552	12.368

KÖPINGEBROSugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	16.5600	
Sub-blocks	36	15.9594	0.443318
Varieties	99	44.0000	
Error	259	77.3360	0.298595

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	17.5100	
Sub-blocks	36	4.0161	0.111559
Varieties	99	65.1250	
Error	261	0.0009	0.000003

K⁺ + Na⁺ content meq

Source of variation	df	Sums of squares	Mean square
Blocks	3	23.7275	
Sub-blocks	36	6.9591	0.193309
Varieties	99	27.8037	
Error	261	19.8261	0.075962

 α -amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	3	451.8398	
Sub-blocks	36	884.9199	24.581
Varieties	99	3284.0000	
Error	261	1345.6152	5.156

Appendix 2Analysis of variance, 1976

Experiment I

SÄBYHÖLMSugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	6.4561	
Sub-blocks	28	17.7444	0.633727
Varieties	63	45.9131	
Error	161	42.4021	0.263367

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	4.8125	
Sub-blocks	28	3.5881	0.128145
Varieties	63	57.0156	
Error	161	5.6463	0.023070

K⁺ + Na⁺ content, meq

Source of variation	df	Sums of squares	Mean square
Blocks	3	5.6484	
Sub-blocks	28	8.2935	0.296196
Varieties	63	49.2930	
Error	161	8.6128	0.053495

α- amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	3	18.2969	
Sub-blocks	28	340.5390	12.1621
Varieties	63	2370.1872	
Error	161	1263.9140	7.8504

cont appendix 2

HOKOPINGESugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	16.5313	
Sub-blocks	28	18.8362	0.672722
Varieties	63	41.2188	
Error	157	43.0310	0.274083

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	3.8594	
Sub-blocks	28	23.2749	0.831245
Varieties	63	62.4063	
Error	159	8.7720	0.055170

K⁺ + Na⁺ content, meq

Source of variation	df	Sums of squares	Mean square
Blocks	3	18.8359	
Sub-blocks	28	34.8212	1.243612
Varieties	63	59.4834	
Error	159	28.2033	0.177379

α- amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	3	67.7500	
Sub-blocks	28	7954.4672	284.0880
Varieties	63	7553.0000	
Error	159	2715.7808	17.0804

cont appendix 2

N.O. Polder, Holland

Sugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	5	10.1250	
Sub-blocks	42	60.9322	1.450767
Varieties	63	141.0312	
Error	272	72.3646	0.266046

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	5	12.7813	
Sub-blocks	42	12.6243	0.300580
Varieties	63	77.7500	
Error	273	8.1569	0.029879

K⁺ + Na⁺ content, meq

Source of variation	df	Sums of squares	Mean square
Blocks	5	1.9316	
Sub-blocks	42	15.6196	0.371895
Varieties	63	70.5208	
Error	273	44.9748	0.164743

α- amino N content, colorimetric value

Source of variation	df	Sums of squares	Mean square
Blocks	5	32.2188	
Sub-blocks	42	1195.7011	28.4690
Varieties	63	1802.0000	
Error	273	1411.4550	5.1702

cont appendix 2

ROYE, FRANCESugar Yield kg/parc

Source of variation	df	Sums of squares	Mean square
Blocks	3	8.5693	
Sub-blocks	28	15.7850	0.563750
Varieties	63	32.7959	
Error	153	27.6466	0.180697

Sugar content %

Source of variation	df	Sums of squares	Mean square
Blocks	3	2.1406	
Sub-blocks	28	5.9216	0.211485
Varieties	63	78.3281	
Error	153	28.3128	0.185051

K⁺ + Na⁺ content, meq

Source of variation	df	Sums of squares	Mean square
Blocks	3	4.5264	
Sub-blocks	28	11.0527	0.394740
Vatieties	63	60.8174	
Error	153	57.8926	0.378383

α- amino N content, colorimetric value

Source of variation	df	Sums of squares	Maen square
Blocks	3	1105.0000	
Sub-blocks	28	963.4921	34.4104
Varieties	63	12771.4992	
Error	153	9290.2576	60.7206

Appendix 3t-values 1973

<u>Tester 1+2</u>	Sugar yield	Pol%	K+Na	α -amino N
11x12 Säbyholm	0.71	3.78 ^x	1.62	0.89
Hököpinge	1.50	9.43 ^{xx}	0.22	1.33
Köpingebro	0.52	0.77	0.67	4.60 ^{xx}
13x14 Säbyholm	0.57	1.14	5.48 ^{x(x)}	0.36
Hököpinge	0.82	0.40	2.46	0.43
Köpingebro	4.57 ^x	12.48 ^{xx(x)}	0.93	1.09
<u>Tester 1+3</u>				
11+12 Säbyholm	3.43 ^x	4.77 ^x	4.87 ^x	0.80
Hököpinge	0.50	3.05 ^(x)	1.04	0.69
Köpingebro	3.57 ^x	8.86 ^{xx}	1.06	3.28 ^x
13x14 Säbyholm	5.48 ^{x(x)}	7.37 ^{xx}	3.82 ^x	4.83 ^{xx}
Hököpinge	2.61	9.71 ^{xx}	3.62 ^x	2.29
Köpingebro	2.26	8.09 ^{xx}	0.73	0.73
<u>Tester 2+3</u>				
11x12 Säbyholm	3.26 ^x	0.43	1.06	2.46
Hököpinge	3.53	12.11 ^{xx(x)}	0.11	0.16
Köpingebro	4.91 ^x	10.15 ^{xx}	1.66	6.05 ^{xx}
13x14 Säbyholm	0.13	0.96	3.21 ^x	4.02 ^x
Hököpinge	2.82	1.47	1.42	2.13
Köpingebro	0.28	3.96 ^x	0.73	1.82

Appendix 4t-values 1976

<u>Tester 4+5</u>	Sugar yield	Pol%	K+Na	α -amino N
F ₁ (15x16) Säbyholm	0.39	5.56 ^{x(x)}	1.16	2.06
Hököpinge	2.90	1.15	0.67	2.45
N.O. Polder	0.15	2.40	1.41	3.41 ^x
Röye	1.34	0.57	0.52	1.99
 <u>Tester 6+7</u>				
F ₁ (15x16) Säbyholm	3.03	1.13	5.57	1.89
Hököpinge	2.25	1.90	0.91	2.12
N.O. Polder	0.79	8.07 ^{xxx}	0.73	1.42
Röye	0.59	1.26	1.57	0.27

Appendix 5

Analysis of variance

Experiment II

<u>Sugar yield</u>	df	S.S.	mean square
Blocks	7	2.4126	0.3447
Varieties	15	328.4746	21.8983
Error	87	18.0779	0.2078
Total	109	348.9650	

Pol %

Blocks	7	3.4258	0.4894
Varieties	15	116.4375	7.7625
Error	87	16.2109	0.1863
Total	109	136.0742	

Beet weight

Blocks	7	88.9375	12.7054
Varieties	15	12268.4368	817.8957
Error	87	732.4375	8.4188
Total	109	13089.8112	

K+Na

Blocks	7	1.6445	0.2349
Varieties	15	97.9922	0.5328
Error	87	7.5742	0.0871
Total	109	107.2109	

Nitrogen

Blocks	7	358.3750	51.1964
Varieties	15	10770.5616	718.0373
Error	87	1273.0000	14.6322
Total	109	12401.9360	

Appendix 6

Experiment II

Error terms for estimates of gene effects

	Sugar yield dt/ha	Sugar %	Root Yield dt/ha	K ⁺ content meq	Na ⁺	α - amino N content col.value
m = $\sqrt{8}^2$	5.20	0.43	32.77	0.28	0.14	3.82
a = $\sqrt{20}^2$	7.23	0.61	46.33	0.40	0.20	5.41
d = $\sqrt{100}^2$	16.27	1.36	103.73	0.89	0.44	12.10
aa = $\sqrt{80}^2$	14.57	1.22	92.77	0.79	0.40	10.82
ad = $\sqrt{30}^2$	8.92	0.75	56.83	0.48	0.24	6.63
dd = $\sqrt{160}^2$	20.56	1.73	131.19	1.12	0.56	15.30

t-values

<u>P</u>	<u>t</u>
5 %	2.36
1 %	3.50
0.1 %	5.41

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